Proceedings of
the United States
National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 125 1968 Number 3658

Interspecific Competition in the Tropical Rain Forest: Ecological Distribution Among Lizards at Belém, Pará

By A. Stanley Rand and Stephen S. Humphrey [1]

The ecological differences between sympatric species have proved useful foci for ecological studies, particularly those with an evolutionary viewpoint. The information provided by such studies is relevant to considerations of interspecific competition and to the problem of the causes of tropical species diversity. In general, it is assumed that a species' closest competitors in an area are its nearest relatives. This is probably true within generic and specific groups, but, as this study suggests, it may not be true for higher categories.

Studies on the ecology of sympatric lizards (usually restricted to sympatric congeners) have been made at several localities by various workers, among them Milstead (1957), Inger (1959), Collette (1961), Rand (1964). Little has been published about the ecology of the lizards of lowland tropical forests and almost nothing about those in the rain forests of the Amazon. The study most comparable to the present one is that of Sexton, Heatwole, and Knight (1964) in Panama.

[1] Rand: Smithsonian Tropical Research Institute, Balboa, Canal Zone; Humphrey: 612 Louisiana St., Lawrence, Kansas.

As a result of the observations made in conjunction with other field studies, the authors have collected considerable information about the natural history of lizards in the vicinity of Belém, Pará, Brazil. Some of this has already been published (Rand, 1965; Rand and Rand, 1966), and additional papers are planned. In this paper we present our data on microdistribution patterns among the common diurnal lizard species and its relevance to possible interspecific competition among lizards. We also present our data on lizard body temperature and their relation to habitat distribution.

The senior author, who has made four trips to Belém, has spent a cumulative total of almost four months there between 1963 and 1966. These visits were all made during the period of May through August, a time of intermediate rainfall. The junior author visited Belém from July through August, 1964, and from June through August, 1965.

The observations reported herein were made in the vicinity of the city of Belém, Pará, at lat. 1°27′S, long. 48°30′W, altitude less than 100 feet. The climate is hot tropical with abundant rain and a marked but not severe or prolonged dry season in the southern winter. The climax vegetation is forest, of which three types are locally recognized: "mata de terra firme" or upland forest; "varzea" or forest that is flooded daily by the freshwater tides; and "igapo" or permanently flooded swamp forest (Ducke and Black, 1953). We were able to sample the first two forests much more adequately than the latter.

In addition to the above, we visited a variety of sites that had been disturbed by man and were in various stages of regeneration—from scattered bunches of grass and bare ground to old second growth.

The main localities where our observations were made are as follows:

Parque do Museu Goeldi – a small patch of forest in the city, the undergrowth much modified and denser than normal because of edge effect in some places, cleaned out in others, but the canopy only slightly disturbed.

Bosque Municipal – a somewhat larger but still small patch of forest in the city, modified in much the same way as the Parque do Museu, but less so.

Utinga and Agua Preta – localities in the preserve around the city water supply on the edge of the city, which include "mata de terra firme," selectively cut but quite good in places, and various ages of second growth from just abandoned "roças" through dense tangles to forest that betrays its second growth nature only in the species composition.

IPEAN and Guama Forest Reserve – localities of "mata de terra firme," "varzea" and some "igapo" forest. A variety of ages of second growth and agricultural situations also were sampled in this area.

The following species were seen frequently enough to provide some idea of habitat distribution: *Gonatodes humeralis*, *Iguana iguana*, *Tropidurus torquatus*, *Plica umbra*, *Uranoscodon superciliosa*, *Polychrus marmoratus*, *Anolis punctatus*, *Anolis fuscoauratus*, *Cnemidophorus lemniscatus*, *Ameiva ameiva*, *Kentropyx calcaratus*, *Tupinambis nigropunctatus*, *Mabuya mabuya*. All are diurnal and together these species include over 99 percent of all the lizards we saw active during the day.

Two geckos, *Hemidactylus mabouia* and *Thecadactylus rapicaudus*, the first a common species, are omitted because they are nocturnal. Also seen only rarely were *Anolis ortoni*, *Amphisbaena alba*, *Crocodilurus lacertinus*, and several microteiids.

We must thank Dr. Dalcy Albuquerque, Director of the Museu Paraense "Emilio Goeldi," and Dr. Robert Shope, then Director of the Belém Virus Laboratory, for their help during our visits to Belém.

We are much indebted to Dr. P. Humphrey of the University of Kansas and Dr. P. Vanzolini of the Departamento de Zoologia, São Paulo, for their field assistance and encouragement and for arranging support for the field work of the junior and senior authors, respectively. We also wish to thank the directors of the Instituto de Pesquisas Experimentacão Agropecuarias do Norte (IPEAN) and the Belém Virus Laboratory for their many courtesies and assistance.

Sphaerodactylidae

Gonatodes humeralis

Habitat.—Found only in the forest and in old second growth in the "mata de terra firme" and, less commonly, in the "varzea." They were not found in the young second growth or in open areas without a closed canopy.

These geckos perch above the ground on the trunks of small to very large trees, on large logs and stumps. They are almost always within one and one-half meters of the ground. Rarely were they seen on twigs or leaves or in small bushes, but most frequently on buttressed trees, trees with loose bark, or many small branches or suckers against the trunk that provide complex hiding places, but they are not restricted to such trees. They may leave a perch to hide in leaves on the ground and sometimes come to the ground to catch food.

Abundance.—This is the most frequently seen lizard in the forest and probably the most abundant. It was most common in the somewhat disturbed areas (Bosque and Parque), where densities of several per 100 square meters were probably reached. In the less disturbed and more extensive forests they were much less common. Usually a single lizard was seen on a tree, occasionally two (a male and female), but seldom more.

FOOD.—Insects and other small invertebrates.

TEMPERATURE.—Probably a nonheliotherm, it was never seen basking, but no temperatures were taken.

IGUANIDAE

Iguana iguana

HABITAT.—Very few of these large lizards were seen but they are reported to be most common along the edges of the rivers. One was seen on the edge of a large clearing. It is quite possible that they live in the canopy of the forest away from clearings and rivers as well as on edges, but they are very difficult to see in such situations. They did well in the forested Parque do Museu Goeldi.

In most forested localities (Panama, Swanson, 1950; Costa Rica, Hirth, 1963; British Honduras, Neill and Allen, 1959), iguanas are highly arboreal lizards as adults, though one occasionally comes to the ground. The juveniles are reported as living closer to the ground. Apparently this is true around Belém for local men who hunt them say that they live on the branches of trees. Those running loose in the Museu Goeldi Parque were seen usually 10–20 meters up in the larger trees.

ABUNDANCE.—We saw them rarely, even when we were examining the river margin. Due to hunting they are probably very shy.

FOOD.—Primarily herbivorous and probably largely eat leaves.

TEMPERATURE.—A heliotherm (McGinnis and Brown, 1966). No temperatures were taken but iguanas in the Parque do Museu Goeldi were seen frequently basking.

Tropidurus torquatus

HABITAT.—Found only in open areas and along the edges of clearings, and not in dense second growth or forest.

These lizards perch above the ground, usually below two meters, on tree trunks, logs, rocks, walls, stumps, etc. They seldom climb above three meters except when frightened and are very rarely seen in bushes, on twigs, leaves, etc. They frequently come to the ground to feed.

ABUNDANCE.—This is the most frequently seen lizard in the open and probably the most common. Only one adult male is seen per perch but sometimes one or two females and several juveniles may be associated with him.

FOOD.—Insects and other invertebrates.

TEMPERATURE.—A heliotherm (fig. 2). It frequently basks and shows difference in posture related to substrate temperatures. (For more detailed data on this species, see Rand and Rand, 1966.)

Plica umbra

HABITAT.—Found only in the forest and older second growth. These lizards occur in the "mata de terra firme" and, at least occasionally, in the "varzea" and are not found in the open or on isolated trees.

Individuals of *Plica umbra* were seen on the trunks and branches of moderate to large trees from close to the ground up to at least several meters. None were seen in bushes or on twigs.

FOOD.—Insects and other invertebrates.

ABUNDANCE.—Moderately common. Seldom were two seen on the same perch, but several times a male and a female were found only a few meters apart, more frequently than we would have expected by chance alone. Perhaps some sort of pair bond is formed.

TEMPERATURE.—A nonheliotherm (fig. 2). No basking behavior was seen.

Uranoscodon superciliosa

HABITAT.—Found only along the shaded margins of streams and lakes where the forest interior comes to the edge of the water in both "mata de terra firme" and "varzea."

Individuals were seen up to two meters high on moderate to large diameter tree trunks and on logs at the edge or in the water, some of which the lizards could have reached only by swimming. They frequently jumped into the water when approached and sometimes dove to the bottom and hid.

ABUNDANCE.—This species is moderately common in its habitat. No more than one individual was seen on a perch.

FOOD.—Insects and other invertebrates.

TEMPERATURE.—A nonheliotherm (fig. 2). No basking behavior was seen.

Polychrus marmoratus

HABITAT.—An animal collector for the Belém Virus Laboratory took large numbers in second growth along the edges of forest. Our few specimens were found in similar places. It is likely that this species also occurs in the crown of the forest, as Rand has seen it in such habitats in Trinidad.

Polychrus can and does climb easily on small twigs and branches.

ABUNDANCE.—Though we saw few individuals, many were taken in the area by the Virus Laboratory collector.

FOOD.—Insects and other invertebrates plus an appreciable amount of plant material.

TEMPERATURE.—Probably a heliotherm (fig. 2).

Anolis punctatus

HABITAT.—In the forest, found in "mata de terra firme" and older second growth; not in "varzea" though this lizard probably occurs there at least occasionally. It was not found in the open, on isolated trees, or in young second growth.

Individuals were seen most commonly on the trunks and branches of moderate to large trees up to four meters. They probably also climb up into the branches and lower crown. One individual was seen once coming to the ground to catch something.

ABUNDANCE.—This is a moderately abundant species; usually single individuals were found, occasionally a male and female were found on the same perch or adjacent perches.

FOOD.—Insects and other invertebrates.

TEMPERATURE.—A nonheliotherm (fig. 2). No basking behavior was seen.

Anolis fuscoauratus

HABITAT.—In the "mata de terra firme," in old second growth and at least edge of "varzea," and not in the open areas on isolated trees or bushes, nor in young second growth.

Individuals were seen sometimes on tree trunks but somewhat more frequently on bushes and slender twigs close to the ground; they were found usually below two meters but occasionally as high as three or four, and also they were seen on the leaf litter on the ground.

ABUNDANCE.—Moderately common. Usually isolated individuals were found, but once a male and tiny juvenile were found on the same tree. There is some suggestion that they group themselves in loose colonies with adjacent home ranges rather than distributing themselves evenly or randomly over the available habitat.

FOOD.—Insects and other invertebrates.

TEMPERATURE.—A nonheliotherm (fig. 2). No basking behavior was seen.

TEIIDAE

Cnemidophorus lemniscatus

HABITAT.—Found in open areas where the vegetation is so sparse that there is bare, unshaded ground exposed between tussocks of grass or bushes and not in the forest or even young second growth. The juveniles seem to occur in the most open parts of the habitat.

The species is terrestrial though individuals occasionally climb short distances up bushes or onto logs and hide in holes in the ground.

Abundance.—Occurring in only a few places but abundant there.

Food.—Insects and other invertebrates.

Temperature.—A heliotherm (fig. 2). Individuals were seen basking and were active only in the heat of the day on sunny days.

Ameiva ameiva

Habitat.—Primarily along edges of clearings in forest and second growth. It ranges out into open areas but seldom far from bushes and other cover, and also into second growth and forest but seldom more than a few meters from an edge. Ameivas turn up in clearings completely surrounded by forest, indicating that they do disperse through the forest.

Ameivas are terrestrial, occasionally climbing on rocks and logs, hiding in holes in the ground and among rocks.

Abundance.—Widespread and common in edge and edificarian situations.

Food.—Insects and other invertebrates.

Temperature.—A heliotherm (fig. 2). Ameivas were seen basking; they are usually active only during the heat of the day and primarily on sunny days.

Kentropyx calcaratus

Habitat.—Primarily in the forest, "mata de terra firme," old second growth, and high spots in the "varzea"; very occasionally individuals were seen in open areas.

Though terrestrial, they not uncommonly were seen climbing upon a log, the base of a tree, or branches of a fallen treetop. They hide in holes in the ground and under logs.

Abundance.—Widespread in the forest but only moderately common.

Food.—Insects and other invertebrates.

Temperature.—A heliotherm (fig. 2). Individuals were seen basking in sun patches on the forest floor; they were active only in the middle of the day and on sunny days.

Tupinambis nigropunctatus

Habitat.—This seems to be a wide-ranging species, moving out into open areas, occurring in second growth and far inside the forest in "mata de terra firme" and "varzea."

Largely terrestrial, it hides in holes in the ground.

Abundance.—Not commonly seen but, because it is hunted, it is very shy.

FOOD.—A variety of animal prey including small vertebrates.

TEMPERATURE.—Probably a heliotherm, as several were seen basking (no temperature records).

SCINCIDAE

Mabuya mabouia

HABITAT.—Most common along the edges of forest and of second growth, it also occurs well inside the forest and out in open grassy situations where hiding places are available. With the possible exception of *Tupinambis*, this has the widest habitat range of all the species considered in this paper.

This species is partly terrestrial, but also it is seen frequently on logs, wood piles, and even short distances up tree trunks. It is one of the few species regularly seen in tall grass areas, where they are seen on tree trunks and on posts that extend above the grass.

ABUNDANCE.—Moderately common, least so inside the forest.

FOOD.—Insects and other invertebrates.

TEMPERATURE.—A heliotherm (fig. 2). Frequently seen basking.

Discussion

The ecological profile given in figure 1 summarizes the microdistributions of the lizards under consideration in the Belém area. No species ranges throughout the whole spectrum of the area though some species certainly are more widely distributed than are others.

Of the habitats studied, the forest is the richest in number of species, but most of the species there are not abundant—at least they are not commonly seen. Some of the species high in the forest canopy and others in the leaf litter are certainly more abundant than indicated by the number of times that we saw them. Restricting consideration to areas where our observations are best, among the species that live on tree trunks near the ground or are conspicuously active on the ground, most of the species in the relatively undisturbed forest seem rarer than those outside it. The localities where most of the forest species were most common—the Parque do Museu and the Bosque Municipal—were places where the canopy was only slightly disturbed but the understory more so and where many things, particularly certain snakes, birds, and mammals that might be predators or competitors, were probably absent.

In the forest habitats not only density of individuals per species, but also total density of individuals of all lizard species taken together seemed less than in some more disturbed areas.

Second growth has a lizard fauna much like that of the forest except that certain species are missing and a few like *Ameiva* are more common. Canopy species, particularly *Polychrus marmoratus*, are seen here, more frequently than in older forest apparently because the canopy is closer to the ground.

Clearings and edges have few species but they are sometimes extremely abundant, particularly *Tropidurus torquatus*. These species are undoubtedly native in areas such as Belém, where rain forest is the climax vegetation, but they also occur in other major habitat areas such as "cerrado," where rain forest is absent. Though the lizards typical of clearings disperse through and even live inside the rain forest (e.g., *Mabuya*), they are never abundant there.

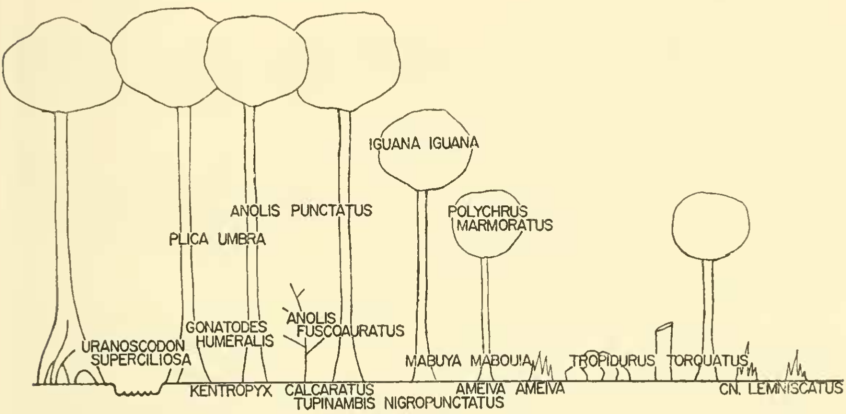

FIGURE 1.—Habitat distribution in Belém lizards: Schematic cross section of Belém habitats from upland forest, with a small forest stream at left, through second growth and grassland to bare ground at right (each species located in area of maximum observed abundance).

There are a number of factors that may be involved in making the forest the environment where the largest number of species occur. Of the environments in the Belém region, the forest comprises the greatest area, it is the most stable on any one site, and it contains the widest floristic diversity and probably the most numerous species of other animals. (These factors were all certainly true before the advent of modern man.) All of these may well be involved in promoting species diversity, and this paper provides no evidence for emphasizing or excluding any of them. Figure 1 suggests that the greater structural complexity of the forest may also be important. There are lizards in the forest occupying structural situations that do not exist or exist only rarely outside the forest. Their restriction to the forest may be, in part, the direct result of the fact that the forest's more complex structuring provides places for the lizards to live.

The physical structures in an environment that a lizard uses as lookouts, hiding places, basking spots, etc., form an important aspect of the

288–727—68——2

environment from the lizard's point of view. They have been called the lizard's "structural niche" (Rand, 1964). When the term was proposed for West Indian anoles, it was found that certain measurements of the perches on which the lizards were seen provided a useful description. Though the concept of structural niche seems useful for Belém lizards, measurements used for West Indian anoles are not sufficient and other environmental parameters must also be considered. In the case of *Uranoscodon superciliosa*, the proximity of water seems important. No system of quantifying the various aspects of structural niches was devised, and they have been described verbally in the foregoing species accounts.

Another set of parameters, in addition to structural niche, must be considered in describing the ecological distribution of lizards. These can be grouped as the lizard's "climatic niche." There are a variety of environmental factors that show parallel gradients here, among them insolation, light, temperature, and humidity. In general, one set of extremes for all these factors in the area is reached on or near the floor of the mature forest, and the other set is reached on the ground in clearings devoid of vegetation. Edges, second growth, and the top of the canopy show intermediate conditions.

The various lizards arrange themselves differently with respect to these gradients. To understand better the relationships of the lizards to the microclimates, we took a number of cloacal temperatures of the former while they were active in periods when the sun was shining; behavioral thermoregulation was possible at this time. In West Indian anoles similar data showed that the lizards in shaded habitats had lower body temperatures than those in open habitats (Ruibal, 1961; Rand, 1964).

The Belém data are a bit more complicated. Figure 2 shows the body temperature plotted against air temperatures taken in the immediate vicinity at the same time. These plots suggest that there are two very different kinds of thermal relationships represented among the Belém lizards: those whose temperature approximates that of the surrounding air and those whose temperature is much above it. A review of observations made of the various species shows that those in the first class were not seen basking while those in the second class were observed with definite basking behavior. Regarding this behavior, it seems safe to conclude that the high temperatures of the second group are due to behavioral thermoregulation and that they are heliotherms while the other group is not—at least at the ambient temperatures observed. (Since their temperature approximates the air and there is no evidence that they use substrates for thermoregulation, we prefer not to use "thigmotherm" but rather the more neutral "nonheliotherm.")

There is a definite relationship, but not unvarying, between thermal relationship and habitat used. The nonheliotherms are all inside the forest, and this is thermally the most constant habitat. The heliotherms occur in the more extreme environments in clearing, second growth, and canopy. One species of heliotherm, however, is almost entirely restricted to the area within the forest (*Kentropyx*), where it basks in the numerous patches of sun that reach the forest floor.

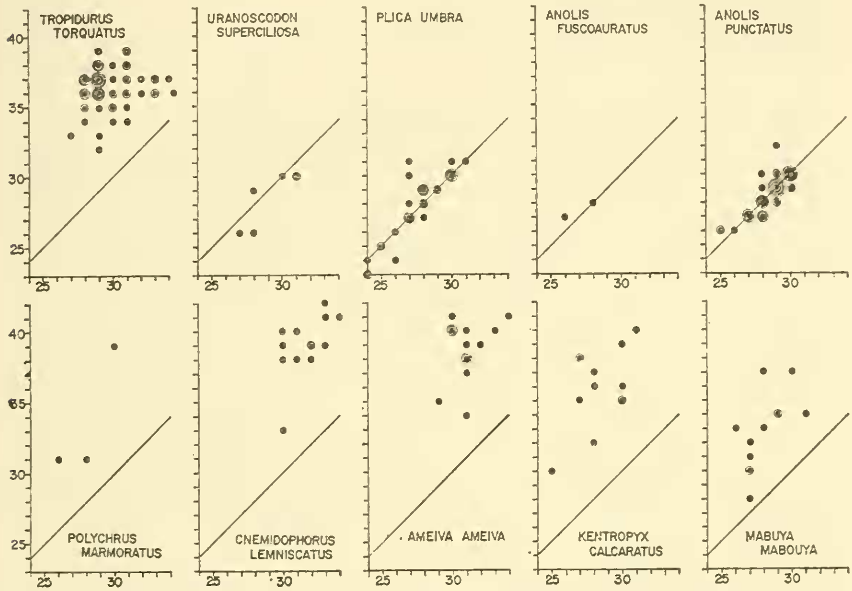

FIGURE 2.—Temperature relationships in Belém lizards: Cloacal temperature plotted against ambient air temperature at time of capture (temperatures in centigrade of just-captured lizards in natural habitat during day).

It should be noted from figure 2 that, under the conditions tested, the nonheliotherms in the forest are about as homeothermic as are the heliotherms that practice behavioral thermoregulation outside the forest (see Rand and Rand, 1966, for details of thermoregulatory behavior in *Tropidurus*). It certainly seems likely that the body temperatures of the open habitat animals would fluctuate much more than they are observed to do if the lizards did not practice some sort of thermoregulation. These data suggest that, if heliothermy has evolved to increase homeothermy rather than to produce high body temperature per se, then it has probably evolved in response to the fluctuating conditions in open environments. The data also suggest that the high body temperatures observed in heliotherms reflect the general principle that, if an animal is to be diurnally active, heating is easier to accomplish than cooling in an area of high insulation.

The foregoing indicates that *Kentropyx* may be a recent invader of the forest from a macroteiid ancestor that was adapted basically to living in open habitats.

Though *Kentropyx* is the only primarily forest heliotherm, other heliotherms like *Tupinambis* and *Mabuya* also occur there. Low eccritic temperatures usually are associated with low temperature tolerances. Because of this and because the upper threshold of tolerance is usually sharper and more quickly lethal than the lower, it is probably easier and safer for open habitat animals to disperse through the forest than for forest animals to disperse through open habitats.

The role of interspecific competition is a basic problem in animal ecology. One of the reasons for our interest in the distribution of Belém lizards was that the evolution of differences in microdistribution has been suggested as an important strategy in reducing interspecific competition among sympatric lizard species (Rand, 1964; Milstead, 1957; and others). The basis for this suggestion in lizards has come usually from studies of sympatric congeners, but there seems no reason that it could not occur between sympatric relatives of different genera. Ecologists(e.g., MacArthur, Recher, and Cody, 1966) who attempt to discover environmental parameters that will predict bird species diversity seem to be assuming that a phylogenetic group as large as birds can be treated as an ecological unit for these purposes. We can make a similar assumption about the Belém lizards but, as we will show, it is probably wrong.

The clearest cases wherein differences in microdistribution can be associated with interspecific interactions are those wherein two or more species occur in the same area, utilize the same structural niche, and replace one another in different habitats or different climatic niches. The only case of such replacement suggested by the distributions plotted in figure 1 is the three smaller macroteiids. There is some overlap between these, but each species reaches its maximum abundance in a different environment: *Cnemidophorus* in the bare open patches, *Ameiva* in the edges and second growth, and *Kentropyx* in the forest. All three have similar foraging habits and could well compete if they occurred syntopically.

There are suggestions that size may be playing a role in reducing interaction between overlapping species. This is a strategy much seen in birds (Schoener, 1965, and others). In general, larger lizards take larger prey and this tends to reduce food competition among species of different sizes. In the Belém lizards, the very large macroteiid *Tupinambis nigropunctatus* widely overlaps *Ameiva ameiva* and *Ken-*

tropyx calcaratus. *Tupinambis* is several times the size of the others and as an adult takes much larger food. Another suggestive case is the two forest *Anolis* that occupy very similar structural and climatic niches but differ sharply in size. The third case is the difference between *Polychrus* and *Iguana*, the two lizards of the tree crowns. It seems unlikely that this size difference is related to food competition since *Iguana* is largely and *Polychrus* is partly herbivorous.

There is no evidence of the sort of temporal replacement during the day that Inger (1959) recorded in forest skinks in Borneo. Diurnal versus nocturnal replacement (perhaps involving the large nocturnal trunk gecko of the forest, *Thecadactylus rapicaudus*) is possible, but it is an unstudied problem.

The only major diet difference we now know (our examination of stomach contents has been limited and casual and there is much still to be learned) lies between the two species that regularly take a considerable amount of leaves and flowers, *Iguana iguana* and *Polychrus marmoratus*, and the remainder, which take largely or exclusively animal food. This diet difference plus the difference in structural niche separate the two herbivorous species very sharply from the rest.

To return to microdistribution as a mechanism for reducing species competition, there is considerable difference among species with respect to structural niches as there is with respect to climatic niches. Taken together, the microdistributions (fig. 1) do not show a regular pattern of replacement of one lizard by another because of the presence of overlaps between species (e.g., *Plica umbra* and *Anolis punctatus*) and of gaps between others (e.g., *Uranoscodon* and *Tropidurus torquatus*) in distribution. Since there is a lack of regular replacement, microdistribution does not suggest itself as an important factor in reducing interspecific competition among the lizards in general, though it may be so between certain species. As we have discussed, our observations on other strategies for reducing possible interspecific competition suggest that, even when all are considered together, no regular pattern of ecological separation among species appears. We are left with the impression, which we cannot prove rigorously, that the relationships of the lizard species to each other are not the over-riding factors in shaping their ecologies.

There are several possible explanations. It may be that our data are so incomplete that we have been given a completely erroneous impression. Further study may show that other species occur at Belém. This may fill the gaps in our picture and reveal differences among common species that would eliminate the apparent overlaps. Certainly, much more is to be learned and the latter possibility cannot be eliminated, but, if for no other than heuristic reasons, it cannot be accepted as the only possibility.

There are two other possibilities not mutually exclusive that seem to us more likely. One is that lizards do not make an ecological unit. They, as a group, do not occupy a "lizard niche" that is subdivided among them; rather, the broad niche or niches that lizards occupy are occupied also by organisms of widely differing phylogenetic relationships with the result that several lizards in the same habitat may each have as its close competitors animals that are not lizards at all but other vertebrates or even invertebrates. It may not be coincidental that the most convincing studies of interspecific competition and mechanisms for reducing it in lizards come from the arid areas of North America and from those areas of the West Indies where lizards are very abundant both as individuals and species and play an important role in the trophic ecology. Certainly, one has the impression in the Belém area that inside the forest the disappearance of all lizards would not greatly upset the forest ecological economy if at all.

The relative rarity of lizards in the Belém forests suggests another possible explanation for the apparent lack of regularity in interspecific relationships. This is that populations of lizards are held at such low levels (perhaps by predation) that the populations never reach densities wherein interspecific competition for food or space occurs. It may be relevant that forest lizards are most common in the park areas, where many of the larger predatory birds, mammals, and perhaps snakes are rare or absent; these are also areas where the number of competitors may also be reduced.

Certainly, it is striking how little agonistic behavior one sees among iguanids in the Belém forests. This is in contrast to desert iguanids and those in the West Indies, where fighting or displaying between males is a common sight. One has the impression that the problem the forest lizards are usually faced with is not that of spacing out the population to avoid overcrowding but rather that of bringing together mates at the proper time. Among *Plica umbra*, *Anolis punctatus*, and *Gonatodes humilis*, we have the impression that we found individuals of the opposite sex near one another more often than we would have expected on chance alone. It may be that these lizards form pairs or at least that males and females permanently establish adjacent or overlapping home ranges in preference to living solitarily. The absence of territorial defense and the large amount of potential home range that seems unoccupied suggest that population densities are so low that direct intraspecific competition for exhaustible resources is nonexistent, and it also suggests that probably there is no interspecific competition between most lizard species and, consequently, no selection pressure for mechanisms that would reduce the competition.

If this is true, how can one account for the observed specialization in both climatic and structural niche? The answer is, of course, intraspecific competition in the Darwinian sense. When any species can exploit the available resources (in the broadest sense) more effectively by specializing in part of them, the specialization itself will be selected for unless this selection pressure is countered by selection in other directions. Specialization, by definition, involves loss of ecological amplitude, and selection against specialization is largely generated by temporal fluctuations in environmental conditions that generate a selection pressure for ecological amplitude (Pianka, 1967). In stable habitats—and the inside of the tropical rain forest is one of the most stable—the selection against specialization should be at its lowest.

It may be that low counterselection against specialization, rather than any unusually strong selection pressure for it, has produced some of the extreme specializations we see in tropical forest forms.

We have not the data to choose between these two hypotheses, which, in fact, are not mutually exclusive. It seems most likely that lizards as a block do not occupy a monolithic trophic niche but share a niche in a complex way with many other animals. It also seems likely that the low population levels in the forest lizards result in minimizing the importance of selective forces that arise from interspecific competition between many lizard species.

Conclusions

(1) The Belém area contains several different habitats and no species of lizard studied ranges uniformly through the area. (2) The forest is richest in number of species and the evidence suggests that this is at least in part because of its greater structural complexities. (3) Two types of thermal relationships with the environment are demonstrated by the lizard fauna: the heliothermic in both open and forest habitats and the nonheliothermic inside the forest. The latter show about as much homeothermism as the former because of the relatively low ambient temperature variation inside the forest. (4) The distribution of three species of macroteiid suggests that they replace one another ecologically. A fourth macroteiid that is syntopic with at least two of these is much larger. Two *Anolis* species that are syntopic and occupy very similar structural niches are different in size. (5) These replacements are probably important, but the impression of the distributions is one of irregular overlaps and gaps between niches of species. (6) The apparently unoccupied niches are

probably in part filled by animals that are phylogenetically distantly related to lizards, but ecologically the former should be considered with the latter. The lizards do not make an ecological unit. (7) The low population densities within the forest are such that interspecific competition may be relatively unimportant and ecological specialization may be the result of intraspecific competition for maximum efficiency of resource exploitation. Selection pressure for this must always exist, but the tropical rain forest, because of its great continuous extent and stability, probably generates unusually few counterselection pressures and, consequently, a high relative selection pressure toward specialization.

Literature Cited

Collette, B. B.
1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bull. Mus. Comp. Zool., vol. 125, no. 5, pp. 137–162.

Ducke, A., and Black, George A.
1953. Phytogeographical note on the Brazilian Amazon. An. Acad. Brasileira Cienc., vol. 25, no. 1, pp. 1–46.

Hirth, H. F.
1963. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology, vol. 44, no. 3, pp. 613–615.

Inger, R. F.
1959. Temperature responses and ecological relations of two Bornean lizards. Ecology, vol. 40, no. 1, pp. 127–136.

MacArthur, R.; Recher, H.; and Cody, M.
1966. On the relation between habitat selection and species diversity. Amer. Nat., vol. 100, no. 913, pp. 319–332.

McGinnis, Samuel M., and Brown, Charles W.
1966. Thermal behavior of the green iguana, *Iguana iguana*. Herpetologica, vol. 22, no. 3, pp. 189–199.

Milstead, W. W.
1957. Some aspects of competition in natural populations of whiptail lizards (genus *Cnemidophorus*). Texas Journ. Sci., vol. 9, no. 4, pp. 410–447.

Neill, W. T., and Allen, R.
1959. Studies on the amphibians and reptiles of British Honduras. Publ. Res. Div. R. Allen's Reptile Inst. Inc., vol. 2, no. 1, pp. 1–76.

Pianka, Eric R.
1967. On lizard species diversity: North American flatland deserts. Ecology, vol. 48, no. 3, pp. 333–351.

Rand, A. S.
1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology, vol. 45, no. 4, pp. 745–752.
1965. On the frequency and extent of naturally occurring foot injuries in *Tropidurus torquatus* (Sauria, Iguanidae). Pap. Avuls. Dept. Zool. São Paulo, no. 17, pp. 225–228.

RAND, A. S., and RAND, P.
1966. Aspects of the ecology of the iguanid lizard *Tropidurus torquatus* at Belém, Pará. Smithsonian Misc. Coll., vol. 151, no. 2, pp. 1–16.
RUIBAL, RODOLFO
1961. Thermal relations of five species of tropical lizards. Evolution, vol. 15, pp. 98–111.
SCHOENER, THOMAS W.
1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science, vol. 155, no. 3761, pp. 474–477.
SEXTON, O. J.; HEATWOLE, HAROLD; and KNIGHT, DENNIS
1964. Correlation of microdistribution of some Panamanian reptiles and amphibians with structural organization of the habitat. Caribbean Journ. Sci., vol. 4, no. 1, pp. 261–295.
SWANSON, P. L.
1950. The iguana *Iguana iguana iguana* (L). Herpetologica, vol. 6, pp. 187–193.

U.S. GOVERNMENT PRINTING OFFICE: 1968